

CHEMORECEPTION IN INSECTS AND THE ACTION OF DDT¹

THOMAS SMYTH, JR. AND CHESTER C. ROYS

Department of Biology, Tufts College, Medford 55, Mass.

The unstabilizing action of DDT on many excitable tissues has been firmly established by work in several laboratories (see Roeder and Weiant, 1948, 1951 for references). However, as Roeder and Weiant demonstrated, not all irritable tissues are equally sensitive. At high concentrations of DDT they observed multiple discharges (impulse trains) in cockroach motor nerves, accounting for the tremors observed in isolated legs. At much lower concentrations, motor nerves were unaffected, but certain proprioceptors were selectively unstabilized, also firing short trains or sequences of impulses in place of single spikes. These barrages of sensory input were taken to account for the hyperexcitability and chaotic behavior of insects in the early stages of DDT poisoning.

If the selective action of DDT extends also to different types of receptor, DDT might be a useful tool for the separation and study of the sense modalities mediated by the many varieties of sensilla scattered over the cuticle of insects. Furthermore, since there are strains of housefly highly resistant to DDT, a comparison in different strains of a sense modality affected by DDT might provide information about the sense concerned and the mechanism of resistance to DDT.

With this in mind the action of DDT on chemoreceptors is considered in this paper. An attempt is made to correlate information on receptor function which has been obtained by electrophysiological methods with that derived from behavioral studies.

1. Electrophysiological studies relating chemical stimulation and DDT action

In the course of experiments on chemoreception (Roys, 1954) the vapors of volatile substances such as benzene and toluene were applied in increasing measured concentrations to intact roaches (*Periplaneta americana* L.) and to isolated legs and antennae. It was found that a concentration range in which the free insect appeared to show mild awareness of the chemical also caused a steady increase in the number of afferent nerve impulses recorded from electrodes in the isolated appendage. At higher concentrations, which the animal tried to avoid, electrical activity in the nerves of detached legs changed from a steady high level to a fluctuating pattern of great bursts alternating with periods of relative inactivity. This, and the fact that DDT is capable of producing abnormal impulse trains in certain proprioceptors of the insect leg, suggested an experiment in which the actions of benzene or toluene and DDT were combined.

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Isolated roach or fly legs or segments of legs were pierced by hot-drawn tungsten electrodes. Afferent electrical activity in the leg was amplified and examined with the aid of an oscillograph and loud speaker. Each experiment was also recorded on magnetic recording tape for later study.

To minimize mechanical disturbance of the preparations the chemicals were applied as vapors. DDT was volatilized by heating the crystals in a glass tube and gently blowing the vapor over the preparation, taking care not to overheat the leg. Typical DDT trains recurred quite regularly and were unaffected by bending large spines. However, toluene vapor from an olfactometer had a well defined effect on the DDT trains, increasing their duration and frequency.

The effect is illustrated in Figure 1. The metathoracic femur of a housefly (*Musca domestica* L.) was mounted with an electrode in each cut end and covered with vaseline. The vaseline blanket limited the number of receptors responding to external stimulation, and provided a relatively simple pattern of afferent discharge. In the untreated preparation (1A) a single fiber was firing somewhat irregularly. Exposure to the vapor of toluene (1B) brought in several other fibers and increased the frequency of discharge, which had not quite returned to the resting level after the toluene had been removed (1C). Three minutes after a brief exposure to DDT vapor (1D) a sequence of well-defined DDT trains appeared, taking the place of the sequence of single spikes. However, the number of exposed receptors had been so reduced by the vaseline coating that the DDT trains were relatively infrequent in the absence of toluene. Exposure of the DDT-treated preparation to toluene (1E) was found to influence the repetition frequency of whole trains in a manner similar to the way in which it affected the single action potentials before DDT treatment. Also, several previously inactive fibers, also firing in trains, were brought by toluene to the discharge level so that the total number of impulses in unit time for a given toluene concentration was much greater after treatment with DDT. Removal of the benzene (1F) led to a return to a condition in which, once more, only occasional trains appeared. The effects of toluene can be obtained and removed many times on the same preparation, but the effects of DDT are irreversible under these conditions. Similar results were obtained from the tarsi of roaches.

This gives weight to the suggestion (Roeder and Weiant, 1948) that DDT in itself does not stimulate receptors, but changes their pattern of response to normal stimuli from discharge of single spikes to repeated high frequency trains of impulses. As with proprioception, one might expect DDT poisoning to produce excessive reflex behavior due to the increased numbers of impulses delivered by each chemoreceptor at a given level of stimulation. Behavioral confirmation of this is described in the next section.

2. DDT and contact chemoreceptor thresholds

When the tarsi of various insects come in contact with certain "acceptable" compounds, the insects respond by extending the proboscis and attempting to feed. This reflex has been the basis for numerous studies of tarsal chemoreception, notably by Minnich, Frings, and Dethier (see Dethier and Chadwick, 1948, for references). Modifications from their techniques were used in the studies described here.

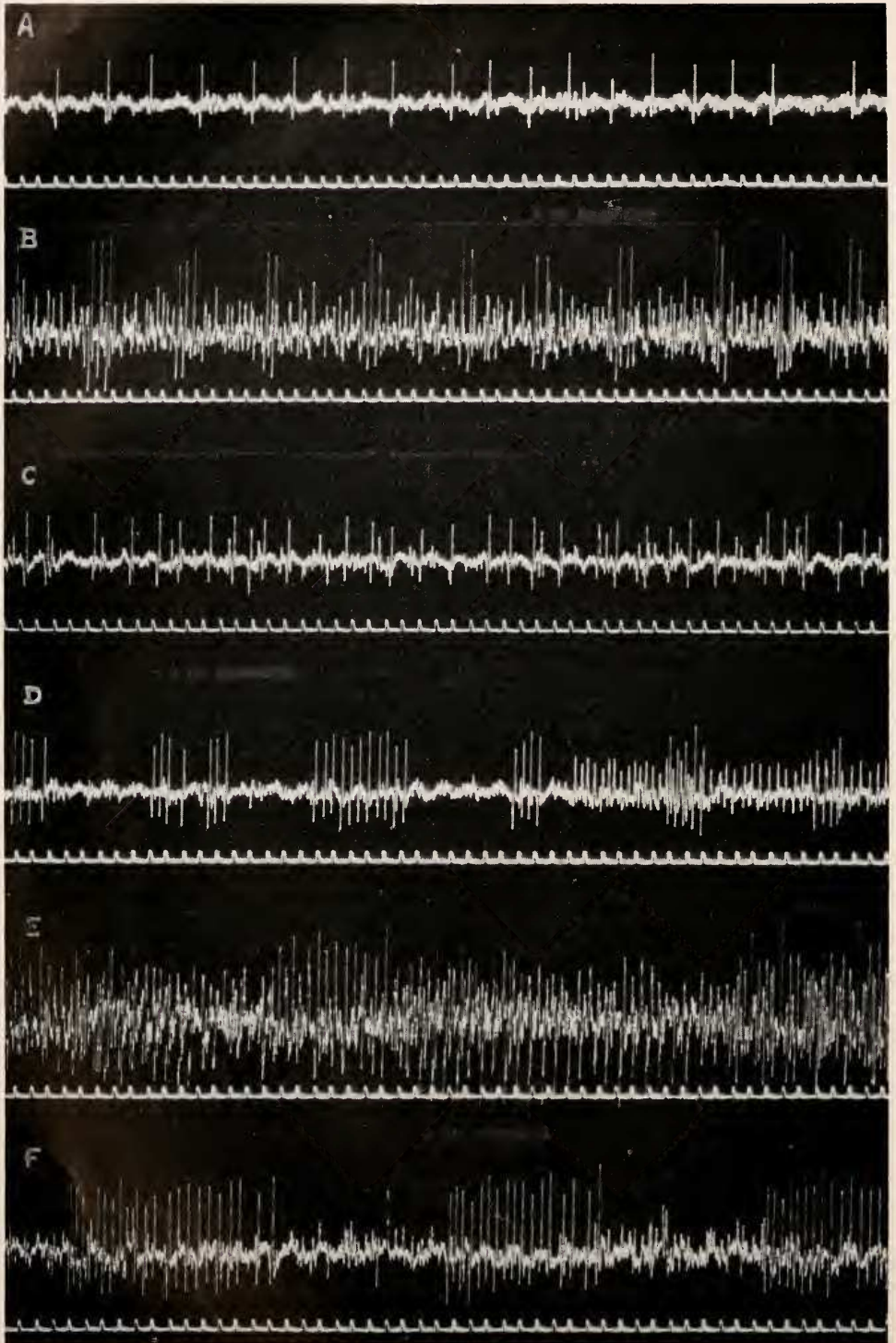


FIGURE 1.

Tarsal thresholds were determined for two strains of houseflies (*Musca domestica* L.), one DDT-sensitive, the other DDT-resistant, obtained from Dr. L. E. Chadwick of the Army Chemical Center, and for DDT-sensitive blowflies (*Phormia regina* Meigen) obtained from Professor V. G. Dethier of the Johns Hopkins University.

The larvae were reared on a milk-yeast-agar medium at 30° C. Pupae and adults were kept at room temperature (21–25° C.). Emerging flies were removed daily and given access to a supply of 0.1 *M* sucrose. One day later flies to be used were anesthetized with carbon dioxide and attached by their wings to paraffined sticks. When volatile substances were to be tested, olfactory receptors (antennae, palpi and labellum) were extirpated at this time.

Thresholds were determined the following day by one of several procedures. For sucrose acceptance thresholds the flies were first allowed to drink distilled water to repletion. Each fly was then held for two seconds with its tarsi in one of a series of sucrose concentrations. Proboscis extension within this time constituted a positive response. If the fly failed to respond, it was tested on 0.1 *M* sucrose, a concentration to which all normal flies should respond. Response here was taken to indicate that the fly was normal in so far as its feeding response was concerned, and it was scored as negative to the previously tested solution. Flies not responding to 0.1 *M* sucrose were considered to be injured or grossly abnormal and data on them were discarded.

Rejection thresholds for NaCl and ethanol were determined in two ways. The various concentrations of the compound to be tested could be made up in 0.1 *M* sucrose, in which case the rejection threshold was the salt or alcohol concentration just preventing the normal positive response to sugar. Or, having denied the flies water before testing, the solutions could be made up with distilled water (no sucrose), the rejection threshold obtained being relative to the thirstiness of the flies. Thresholds against water were much more difficult to obtain than thresholds against sugar, but a few were determined to show whether the action of DDT on sugar receptors masked an effect of DDT on "rejection" chemoreceptors. In either case the flies were given ten seconds to reject the test solution. Extension through the ten second period constituted a positive response (sub-threshold salt or alcohol). Flies failing to respond, or retracting within ten seconds, were checked for two seconds on 0.1 *M* sucrose or distilled water, depending on the type of experiment. Flies responding here were classed as negative; those not responding at all were discarded. In no case was a fly allowed to drink a test solution.

The usual method of DDT application was to place the tarsi of the mounted flies in contact with a DDT-coated glass plate for five minutes immediately before testing. Sensitive houseflies developed symptoms of poisoning seven to eight minutes after exposure at the concentration used—0.01 milligram DDT per square

FIGURE 1. The effect of toluene vapor on electrical activity in afferent fibers of the housefly femur before and after treatment with DDT. A. Untreated preparation. B. Increased activity upon exposure to toluene vapor. C. Toluene vapor withdrawn. D. Three minutes after exposure to DDT vapor. E. Effect of toluene vapor on the DDT-treated preparation. F. Toluene vapor withdrawn, leaving only DDT trains. Time marks, 10 millisecond intervals. For further explanation see text.

centimeter (approx. 9.3 mg./sq. ft.) deposited from acetone solution. To determine whether the cuticular surface of the sensitive tarsal chemoreceptor was the site of selective action by DDT, the insecticide was also applied to another area. In these experiments the meso- and metathoracic legs were immobilized in paraffin ("two-leg flies") and a small droplet of DDT in mineral oil (one milligram per milliliter) was applied to the tip of the abdomen. To answer the question of whether cuticular impermeability barred DDT from the receptors of resistant flies sucrose thresholds were determined for flies injected with DDT. Sensitive as well as resistant flies were run as a check on the method. One per cent DDT in tri-ethylene glycol was serially diluted with Pringle's insect Ringer to 10^{-5} for

TABLE I
Tarsal sucrose acceptance thresholds of Musca and Phormia with and without various DDT treatments

Species	DDT sensitivity	Treatment	Median molar threshold	Log median threshold	Standard error log threshold	Regression response on concentration	Standard error regression	Total flies tested
a. Musca	sensitive	control	.0067	-2.176	±.039	2.00	±.16	479
		tarsal DDT	.00074	-3.129	.029	1.37	.24	201
b. Musca	resistant	control	.0043	-2.365	.068	1.59	.21	204
		tarsal DDT	.0041	-2.389	.063	1.79	.25	204
c. Phormia	sensitive	control	.0020	-2.689	.053	2.16	.28	192
		tarsal DDT	.00043	-3.363	.083	1.50	.22	162
d. Phormia (2-leg)	sensitive	control	.013	-1.887	.046	3.80	.77	66
		tarsal DDT	.0026	-2.585	.055	3.29	.77	64
		abdominal DDT	.0029	-2.536	.059	2.90	.72	63
e. Musca	sensitive	tarsal DDT	.0047	-2.331	.075	1.24	.19	216
		injected DDT	.012	-1.913	.053	2.34	.32	216
f. Musca	resistant	tarsal DDT	.0054	-2.271	.055	2.35	.30	132
		injected DDT	.0064	-2.191	.058	2.98	.37	132

resistant flies and 10^{-6} for sensitive flies; 0.004 milliliter of this was injected into the thorax, giving doses of 0.04 and 0.004 microgram per fly, respectively.

Whenever there were sufficient data, a probit analysis of the results was made (Finney, 1952). In other cases median thresholds were estimated by graphic interpolation.

The tarsal chemical thresholds obtained are listed in Tables I and II. DDT lowered the tarsal sucrose threshold of DDT-sensitive houseflies by a factor of nine, but did not affect the response threshold of resistant flies (I,a,b). The sucrose threshold of blowflies was also strikingly lower following exposure to DDT (I,c).

The method of application was unimportant; DDT picked up by the tarsi, applied in mineral oil to the abdomen (I,d) or injected in saline suspension (I,e) all increased the sensitivity to sucrose. The sucrose thresholds (I,e) of sensitive houseflies following tarsal and internal application of DDT differ by a factor of

three, and at first sight suggest that injected DDT was only half as effective as externally applied DDT in lowering the sucrose threshold. However, this difference can be accounted for by the fact that thresholds of the injected flies varied over a wide range. Only about half of the injected flies appeared to be effectively treated, their thresholds and variance being similar to those of the tarsally poisoned flies in this group. The remaining flies had thresholds scattered about a concentration some nine times higher, but with a similar variance. Possibly the large amount of solution injected interfered with circulation, preventing the transport of DDT to the receptors. The thresholds of flies in I,e and I,f cannot be

TABLE II

Tarsal salt and alcohol rejection thresholds of Musca and Phormia tested against water or sucrose solutions, with and without tarsal application of DDT

Species	DDT sensitivity	Treatment	Median molar threshold	Log median threshold	Standard error log threshold	Total flies tested
<i>NaCl against 0.1 M sucrose</i> a. Musca	sensitive	control	1.7	0.22		125
		tarsal DDT	1.7	0.23		70
b. Phormia	sensitive	control	1.4	0.161	±.019	110
		tarsal DDT	1.3	0.130		.018
<i>NaCl against water</i> c. Musca	sensitive	control	1.0	0.00		30
		tarsal DDT	1.2	0.12		51
<i>Ethanol against 0.1 M sucrose</i> d. Musca	sensitive	control	6.8	0.83		59
		tarsal DDT	4.4	0.65		34
e. Musca	resistant	control	3.5	0.55		20
		tarsal DDT	2.5	0.40		21
f. Phormia	sensitive	control	1.7	0.22		44
		tarsal DDT	1.8	0.25		44
<i>Ethanol against water</i> g. Musca	sensitive	control	1.1	0.05		15
		tarsal DDT	1.1	0.05		13

compared with those in I,a and I,b, it being a common experience in such tests that thresholds vary widely in different experimental groups.

The threshold of resistant flies was unchanged (I,f), even when DDT was injected in amounts sufficient to poison some individuals. In no case did DDT treatment significantly affect a salt or alcohol threshold, either tested against sucrose or against water (Table II).

It should be pointed out that absolute threshold values changed from time to time over a considerable range, even though an attempt was made to maintain standard rearing and test conditions. The comparisons indicated in Tables I and II represent data collected in concurrent experiments where alternate flies in the

same population were given the various treatments. Some of the data represent lumping of results from duplicate experiments run within a period of a few days. In all these cases the individual experiments were consistent with each other, although slight displacements of the absolute thresholds increase the standard errors. Considerable other data not suitable for inclusion in the tables substantiate the results reported.

In spite of an intensive search in several laboratories there is no electrophysiological evidence of afferent nerve impulses from chemoreceptors concerned with detection of sugar or other substances producing proboscis extension by flies. Nevertheless, perception of such stimuli can be understood only in terms of increased or decreased receptor activity. Because DDT in general increases the activity of irritable units if it affects them at all, and because it also increases the fly's sensitivity to sugar, the simplest explanation of these observations is that there must be chemoreceptors which respond to acceptable compounds by sending nerve impulses more frequently to the central nervous system. DDT would then act by converting each single impulse to a group or train of impulses (Fig. 1), increasing the message rate relative to the supply of information. Chances for central summation, either spatial or temporal, would be increased, and so therefore the likelihood of response. In other words, assuming a steady central excitatory state, if proboscis extension be elicited by a sensory input consisting of a certain number of impulses in a given time interval from a specific group of receptors, then the tendency to high frequency repetition caused by DDT should make possible the requisite input from a smaller number of receptors, and hence from a lower concentration of stimulant.

A somewhat more complicated but also plausible explanation is that the chemoreceptors detecting acceptable compounds are relatively DDT-insensitive. The sensitizing action of DDT would then have to be on some other receptor system, activity in which would facilitate the proboscis response. This idea will be referred to again.

Although salt and alcohol are representatives of different human taste modalities and may also be different to the insect, both are rejected and they can be discussed together here. In no instance was a rejection threshold affected by DDT treatment. Yet, the preceding electrophysiological observations indicate that DDT increases the afferent response to chemical stimulation. Moreover, as demonstrated by the rejection thresholds against sugar compared with those against water, rejection thresholds depend on the intensity of the opposing acceptable stimuli, high sugar concentrations raising the rejection thresholds. And, sugar is a more effective stimulus following DDT treatment. Therefore, DDT must increase the activity of "rejection" receptors to an extent that balances its effect on sugar receptors or their adjuncts. Furthermore, acceptable and unacceptable compounds must act primarily on different receptor units and not in opposite manner on one receptor type. Otherwise one would have to attribute to DDT simultaneous stabilizing and unstabilizing actions on the same cell in order that the rejection threshold remain unchanged. This confirms Dethier's (1953) conclusion that there must be at least two varieties of chemoreceptors on fly tarsi.

DDT applied to the surface of the abdomen or injected into DDT-sensitive houseflies and blowflies lowered sucrose thresholds just as it did when applied to the tarsi. Because neither externally applied nor injected DDT affected the

thresholds of DDT-resistant flies, it seems reasonable to say that cuticular impermeability is not solely responsible for the resistance of this strain. Rather, resistance must include some intrinsic mechanism by which the receptors are protected from the unstabilizing action of DDT. Pratt and Babers (1953) reached a similar conclusion for the thoracic ganglion after studying its DDT-sensitivity in susceptible and resistant houseflies. Although they believe that enzymatic detoxification of DDT is not rapid enough to account for the difference observed between the two strains, it seems possible that a strategic deployment of the protective enzymes to the primary sites of DDT action could account for such resistance.

3. Surface texture and the proboscis extension reflex

In the course of tarsal chemoreception tests on *Phormia* and *Musca* it was observed that an occasional fly would attempt to feed when placed on a clean, smooth surface, especially during the earliest stages of DDT poisoning. Using surfaces at hand it was found that proboscis extension occurred when the tarsi were placed on smooth glass, Lucite, celluloid, polished metals and glazed kymograph paper, but not on newsprint, rough wood, frosted glass or the investigator's finger or clothing. Proboscis extension being the customary criterion of effective stimulation of the "acceptance" receptors, this behavior seemed worthy of further investigation.

Additional observations were made on 338 houseflies mounted on sticks in the manner previously described. After 24 to 40 hours of starvation (until a good response to water was obtained), they were tested in the following manner. Each fly was held so that its tarsi were in contact with either the smooth or rough side of a piece of frosted glass for five seconds, then transferred to the other surface. This was repeated, and if no response was evoked the fly was tested on distilled water. When a positive response was obtained with a dry surface, the fly was repeatedly tested for five-second intervals on the two surfaces.

Of 177 flies responding positively to distilled water, one invariably responded to both surfaces, 155 to neither, and 21 discriminated between the two, responding only to the smooth side. None responded preferentially to the rough. A few *Phormia* were later observed to respond to a clean, smooth surface even though satiated with distilled water. Feeding dry powdered sugar one hour before testing did not alter the proportion of flies responding to surface texture. DDT applied in the manner described above increased the level of response to almost all stimuli.

Like most other behavior patterns the proboscis reflex is not solely the product of a single chemical releasing stimulus, but depends on the balance between facilitating and inhibitory influences from a number of sources, *e.g.*, other chemical stimuli, nutritional state, water balance and mechanical excitation. If these secondary stimuli were to produce a sufficiently favorable state of central excitation, it is possible that spontaneous activity from the chemoreceptors could exceed the threshold for proboscis extension. A background of summing activity from many mechanoreceptors stimulated in unison as by a smooth surface might well contribute to a favorable central state. Rough surfaces should stimulate in a more erratic fashion.

DDT could increase the likelihood of feeding response either by amplifying the activity of the chemoreceptors, or by increasing the number of mechanorecep-

tors active at any one time. Although DDT eventually increases the irritability of certain mechanoreceptors and chemoreceptors, the magnitude of its effect on the sugar threshold is probably indicative of an early action on sugar receptors.

One wonders why flies should be more prone to feed on a smooth surface. Perhaps the vacuum-cleaner type mouth part functions more efficiently here. Also, the resemblance between smooth surfaces and a water surface may be great to a fly.

4. Perception of DDT by houseflies

The fact having been established that DDT can increase the sensitivity of various receptor systems to their appropriate stimuli, there remained an interesting question as to whether the insect can detect DDT itself. Ability to do so would make possible a behavioral type of resistance through selection of strains avoiding the chemical. A rather surprising answer to this question was obtained by

TABLE III
Distribution of houseflies in petri dishes between chemically impregnated and control (acetone-treated) papers

Compound tested	DDT sensitivity	Flies on treated paper	Flies on control paper	Chi-square	Probability	Total flies on paper	Total possible flies on paper
DDT	sensitive	1336	1136	16.2	.01	2,472	12,100
DDT	resistant	792	808	0.16	.5-7	1,600	9,040
DDT	sensitive	611	506	9.86	.01	1,117	4,800
DDE	sensitive	558	547	0.110	.7-8	1,105	4,800
1,1-bis(p-chloro-phenyl) ethane	sensitive	564	575	0.106	.7-8	1,139	4,800

confining flies in chambers with two pieces of paper, one containing DDT, and recording periodically the distribution of the insects.

The procedure was as follows. Seven-centimeter filter papers were prepared with 0.01 milligram DDT or other test compound per square centimeter deposited from acetone solution. After complete evaporation of the solvent the papers were cut in half and paired with acetone-treated control half circles in the bottoms of clean petri dishes. To keep them in place, the papers were dampened with distilled water. Ten flies were placed in each arena and counts of the number of flies on each of the two test half-circles in each petri dish were made every minute from the eleventh through the twentieth minute after the beginning of the experiment. Clean dishes and fresh papers were used for each test.

Under these conditions sensitive flies exposed to DDT in the course of the experiment did not begin to show overt signs of DDT poisoning until thirty minutes or more after introduction into the dishes. Each dish contained one test and one acetone control paper. Both papers and dishes were arranged according to a Latin square design in order to minimize the influence of external factors such as light and temperature gradients, and bias on the part of the observer.

The results are shown in Table III. In both series of tests the data clearly show that DDT-sensitive flies have a predilection for the DDT-treated surface. DDT-resistant flies show no such preference. However, DDT-sensitive flies fail to discriminate between surfaces treated with DDE (1,1-dichloro-2,2-bis (p-chlorophenyl) ethylene) or 1,1-bis (p-chlorophenyl) ethane and acetone controls. This suggests that the factor in the DDT-treated paper which is the basis for preference is connected with the specific physiological activity of DDT rather than with general physical or chemical properties which it presumably shares with the two relatively non-toxic DDT analogs tested.

Proboscis extension and withdrawal are not the only responses to chemical stimulation of the tarsi. When one of the tarsi touches an acceptable substance the fly turns toward that point and begins feeding. Avoidance of noxious chemicals also occurs. Thus stimulation of contact chemoreceptors initiates orientation behavior related to feeding as well as the feeding reflex itself. Probably, the same receptors control both activities. Since it is apparent that there are different groups of receptors responding to acceptable and unacceptable compounds, the preference of DDT-sensitive flies for DDT could be taken to show that DDT selectively potentiates (by causing impulse trains) the sensory input from "acceptance" receptors during the early stages of poisoning, "rejection" receptors being either less sensitive or slower to respond. On this basis a DDT-treated surface could have an illusory attractiveness to flies when first walking on it. This would account for the increased time spent on such surfaces in the experiment. DDT-sensitive flies, by choosing to spend additional time in DDT-treated areas in a partially treated environment contribute to their own destruction. Through loss of ability to detect the insecticide, relatively resistant flies will come in contact with less DDT and further improve their chances of survival.

GENERAL DISCUSSION

Among the many receptors on the tarsi of flies several types responding to different modalities of stimulation control the feeding response. These include at least two types of contact chemoreceptor (see also Dethier, 1953), activated by acceptable and unacceptable compounds, releasing or inhibiting the feeding reflex and orientation to food. Under conditions of near-starvation a suitable pattern of tactile stimulation can release feeding behavior. Therefore, one may assume that mechanoreceptors modulate the effects of afferent impulses from chemoreceptors, even though touch is not normally the effective stimulus for the proboscis extension reflex.

Such a cooperation between sensory systems should make possible an economy in terms of the number of receptors of each type necessary; a limited amount of cross summation between associated stimulus modalities would increase the effectiveness of each stimulus. A high level of spontaneous activity in unstimulated receptors should increase similarly the effect of stimulation of a portion of the receptor population.

Electrophysiological observations, both those relating to insect mechanoreceptors and those reported here for chemoreceptors, show a background of spontaneous activity. DDT increases the effectiveness of this background by converting single nerve impulses to trains of impulses. The more frequent afferent impulses

which result from normal stimulation are also made repetitive by the action of DDT. Opportunities for summation both within and among modality groups are thus increased.

Observation of DDT-poisoned insects corroborates this interpretation. Shortly after exposure to the insecticide certain response thresholds of DDT-sensitive individuals become lower. A decided hyperexcitability develops, and this gives way to random reflex activity as, presumably, more and more receptors become unstabilized. Uncoordinated locomotor movements and proboscis extension and retraction are characteristic symptoms of this stage of poisoning. In DDT-sensitive flies the effect of DDT on individual receptors is irreversible.

SUMMARY

1. DDT appears not to stimulate sensory endings, but makes them capable of repetitive discharge following stimulation with toluene and benzene.

2. Pretreatment with DDT lowers about nine-fold the sucrose acceptance thresholds of DDT-sensitive houseflies and blowflies. Sucrose thresholds of resistant flies are unaltered.

3. Pretreatment with DDT does not change salt or alcohol rejection thresholds, either against sucrose or water.

4. Under certain conditions clean smooth surfaces can evoke feeding behavior similar to that in response to acceptable chemicals.

5. DDT-sensitive houseflies, given a choice, spend a greater amount of time on DDT-treated areas. Resistant flies do not. Surfaces treated with DDE and 1,1-bis (p-chlorophenyl) ethane are not discriminated from control surfaces.

6. It is concluded that acceptable and unacceptable compounds are perceived through different sets of receptors.

7. The proboscis extension reflex is not controlled by chemoreceptor activity alone, but also by tactile stimuli.

8. The failure of DDT to affect reflex behavior of this strain of DDT-resistant houseflies is not due to failure to penetrate the cuticle, but must be due to some mechanism intrinsic to the nervous system.

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